Lessons from a drought: fynbos on rocky soils at higher altitudes may cope better with climate change

Marc Burman

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Supervisor: Professor William Bond

University of Cape Town

Abstract

Global climate change is taking place, with associated increased drought in the Southern Hemisphere. Bioclimatic models predict that warming and drying of the climate will cause a massive contraction of the range of the fynbos biome in the next 50 years. The 2003/2004 drought (of one in 100 year severity) in the Western Cape is viewed here as putative climate change, and its effects on fynbos vegetation are studied. The long-term rainfall record for the study area was analysed to assess the 2003/2004 drought severity. Species mortality, xylem anatomy and vegetation health were sampled across all woody fynbos species, along an altitudinal gradient and on shallow rocky versus deep sandy soils, in the Agter-Cedarberg, South Africa, in 2005. Most vegetation was healthy (65-67%). Mortality was lower at higher altitude ($p<0.000$), and on rocky soils ($p=0.004$), although the altitudinal trend was very weak ($R^2 =0.0400$). Vegetation condition was classed as poor, based on a 30km road transect. Riparian trees were in very poor condition (7/10 species had >50% canopy death). Xylem anatomy did not correlate with species health, nor did a measure of conductivity. Species response was highly variable, with the genus *Aspalathus* experiencing the highest mortality. Severe drought impacts were highly localised. Pre-drought studies are essential to provide a control for post-drought assessment. Fynbos will change in response to climate change, and predicting extinctions and survival depends on studies of drought tolerance. Such studies are critical in making conservation decisions such as reserve choice.

badly expressed .

Introduction

There is no doubt that global climate is changing (Dore 2005; Midgley et al 2001; IPCC 1996). Surface temperatures are increasing, which alters atmospheric circulation, resulting in changes in precipitation patterns (Dore 2005). Biodiversity is at risk from these changes, as habitats change from altered rainfall patterns. The conservation of biodiversity depends on an understanding of how vegetation reacts to drought, on a physiological and a landscape level. This is important for the development of conservation plans and reserve selection, as areas previously suitable for reservation may become unsuitable in the future, if bioclimatic models are to be believed. Such models have been developed for fynbos in the Western Cape, and predict a possible massive reduction in suitable habitat by 2050 (Midgley *et al* 2003). However, models are assumption-based, and many of the assumptions involved may not apply to all the species and areas modeled. For example, the model does not consider the impact of soil type differences (shallow rocky versus deep sandy) on the ability of plants to survive drought.

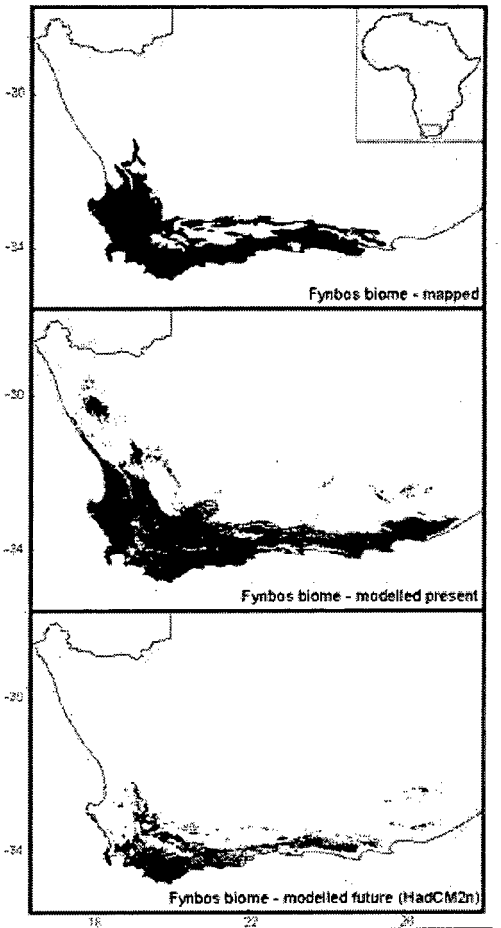

Figure 1. The future size of the fynbos biome is predicted to be much smaller by 2050, with only mountainous regions in the Southern Cape supporting offering suitable habitat. Reproduced brom Midgley *et al.* 2003.

This is the first study that directly investigates the effects on vegetation of putative climate change, in the form of the 2003 / 2004 Western Cape drought, on vegetation in South Africa. Previous studies have observed the effects of drought (for example Milton 1995). The 1990/1991 drought caused a decrease in

perennial vegetation, especially in sclerophyllous karoo bushes, in the Steytlerville Karoo, which reduced the carrying capacity of the area for grazing (Milton 1995). The 2003 winter rains failed almost completely, causing the worst drought in over 100 years. This was followed by another critically dry winter in 2004. However one defines drought, there is no doubt that the period from 2003 to 2004 constituted a period of extreme stress for the vegetation of the Agter-Cedarberg. Drought impacts were noticeable in 2004 in the area, in the form of patchy mortality across the landscape, especially in the spine-leaved woody shrub *Nylandtia spinosa* (William Bond, *personal communication* 2005). It is no longer in doubt that human-induced climate change is taking place (IPCC 1996). Greenhouse gas emissions will increase the average global surface temperature by one to three and a half degrees Celsius by the year 2100 (Kattenberg *et al.* 1996 *in* Hanson & Weltzin 2000).

Ecologists have recently begun to speak out loudly to the public about the threat to South Africa's biodiversity from the projected climate changes over the next 50 years (Midgley *et al.* 2001 – 'The heat is on' booklet). While the predictions are based on simulated models, and must therefore be interpreted with care, it is beyond doubt that there will be climate change. For the fynbos vegetation in the Agter-Cedarberg, it is predicted that in the year 2050, the number of days per year when soil moisture and temperature are suitable for plant growth ('soil moisture days', Midgley *et al.* 2001) will be about half of what they are now (Midgley *et al.* 2001).

Fynbos is a sclerophyllous Mediterranean vegetation type found only on nutrient-poor sandstone soils, which occurs only in the winter rainfall region of the Western Cape. It has exceptionally high levels of species diversity and endemism (Cowling 1992), and has been given high conservation status as a Global Biodiversity Hotspot (Myers *et al.* 2000). The focus area is the northern edge of the extent of fynbos, bordering the semi-arid karoo. Of all ecosystems,

biome boundaries along a moist to semi-arid gradient are thought to be most at risk from climate change (IPCC 1996).

Species richness and the high levels of endemism in the Western Cape are thought to have arisen during a period climatic stability that began in the Pliocene, together with geological stability, steep ecological gradients and fine-scale habitat diversity (Goldblatt 1997). As a result, the component species are neither tolerant of changes in habitat, nor able to disperse rapidly. The rate at which climate change is taking place is much greater than that of species dispersal, colonisation and establishment in new habitats.

In an attempt to understand the risks and to generate contingency planning tools, Midgley *et al.* (2003) used bioclimatic envelope modelling of future ranges of 28 species of *Protea*. The model predicted range contraction for 17 species, 5 extinctions and 11 possible range expansions, associated with an increase in temperature of about 1.8°C over the next 50 years. However, plant habitat varies widely within a species across its range (personal observation), for example in micro-climatic conditions related to the aspect of the site, density of the overstorey and soil type. In ignoring such factors, bioclimatic models may risk over-stating the extent of the threat. In this study I have investigated two such microclimatic factors, specifically the effects of altitude and of different soil type on plant survival and health following the recent drought.

Many factors determine drought tolerance in plants. These include both physiological systems involved in water and gas exchange, the mechanisms and rates involved in life history (carbon assimilation rate, growth rate and season, longevity and reproductive rate), and external factors like land transformation and fragmentation, fire management and grazing practices (McPherson 1995 *in* Hanson & Weltzin 2000). Feedbacks exist between these and plants. For example, an increase in atmospheric carbon dioxide leads to reduced transpiration and thus reduced plant water use (Hanson & Weltzin 2000). Such

feedbacks can have unexpected effects, which complicate bioclimatic model projections.

The most accessible measure of drought susceptibility is conductive tissue anatomy, specifically xylem vessel diameter and density (Tyree & Sperry 1989; February *et al.* 1995). Vessel diameter is correlated to risk of embolism (Tyree *et al.* 1994), through the Hagen-Poiseuille law (which states that conduit conductivity is proportional to radius^4) (Zimmerman 1983). The result is a positive relationship between xylem conductive efficiency, which increases with vessel diameter, and risk of embolism. Studies have shown a strong relationship between xylem conductivity and plant responses to drought (Tyree & Sperry 1989). A recent study of wood anatomy and drought tolerance has shown that plants with thicker, stronger cell walls of xylem conduits and denser wood are more able to withstand water stress (Hacke *et al.* 2001).

An important aspect to consider is that the effects of drought may be cumulative over time: water stress limits the amount of carbon a plant can acquire, causing a reduction in carbohydrate storage, as well as in growth (Chapin *et al.* 1990 *in* Hanson & Weltzin 2003). The effects of a severe drought, or even ongoing moderately low rainfall, may therefore only become apparent some years later. There is the potential in the Agter-Cedarberg for some or all of these impacts to occur, and this should be monitored closely.

Few studies have demonstrated the long-term effects of drought. One of the best examples of long-term damage is of forest trees in the Northwest USA, after a severe drought in the 1950s. There was massive vegetation die-back during the drought, and the affected area (about 8 kilometres wide) had not returned to the pre-drought state by 1998 (Allen & Breshears 1998). The possibility exists that this process has begun at the edge of the range of fynbos, although on the smaller scale of localised, patchy mortality rather than massive dieback.

Drought detection is difficult, and new methods are being developed all the time. These range from observational methods, such as analysis of satellite photography (operational environmental satellites) which can inform on a wide range of vegetation health factors (Kogan 2000), to the more usual analysis of rainfall records. To this end many indices have been developed (Whilhite 2005), such as the Palmer Precipitation Index and the Standardized Precipitation Index (*reviewed in* Guttman 1998 and Roualt & Yves 2003). The Standardized Precipitation Index was used to detect droughts in historical rainfall records for South Africa from 1921 onwards, and eight major droughts were identified, with inter-drought periods of three to 18 years (Roualt & Yves 2003). There has also been an increase in the number of droughts per decade in South Africa over the last 40 years (Roualt & Yves 2003). However, the patterns differ on a global scale: in the Northern Hemisphere, Northeast United States is expected to experience a decrease in long-term droughts (12 months) according to analyses using the Standarized Precipitation Index and modeling (Gao & Robock 2003).

For the purposes of this study a simpler approach has been used, similar to the decile method of Gibbs & Mahler (1967 *in* Hayes 2002), in which the rainfall distribution is arranged into deciles, with the middle deciles being regarded as 'normal'. Here the approach is modified in that drought is regarded as occurring when rainfall of a period is below 75% of the long-term mean (William Bond *personal communication* 2005). The years 2003 and 2004 fall well below this threshold, so the method of detecting drought is less likely to falsely indicate drought for these years.

The aims of this study were, firstly, to assess the impact of the 2003/2004 drought on the fynbos of the Agter-Cedarberg, and, secondly, to discover whether impacts were reduced at higher altitude, or were lower on rocky than on sandy soils. Lastly I present some recommendations for rapid drought detection and assessment. To achieve these aims, I set out to quantify drought impacts on fynbos, by observing the extent of individual plant mortality at 8 sites along an

altitudinal gradient. One might expect low altitude sites to suffer the most from drought because of the additional heat stress. Alternatively, species response to drought may be less variable along gradients, if each is adapted to the particular conditions of its habitat. Secondly, I compared drought mortality on rocky versus sandy substrates. Lowland fynbos occurs mostly on deep sandy soils. Sandy soils are less good at retaining moisture than clay or rocky soils, so that in times of drought they dry out sooner and more completely than more clayey or rocky soils. Plants might therefore suffer greater water stress on sandy than on rocky soils. Lastly, I conducted road-side transects of vegetation health to evaluate the method as a tool for rapid drought assessment.

Method

Rainfall records from 1870 to 2005 for Clanwilliam and 1898 to 2005 for Mertenhof (a weather station in the Biedow Valley, about 25km East of the study area) were obtained from the South African Weather Service. To determine the severity of the 2003/2004 drought I used the approach in which a drought is considered to be an extended period of rainfall falling below 75 percent of the long-term mean rainfall. In Clanwilliam and Mertenhof peak rainfall occurs in June, with July receiving the second highest (**Figure 3**). Hence, for plants adapted to the climate in this region, it can be supposed that rainfall failure up to the end of July would constitute a serious threat to growth and survival. In the analysis here I used the rainfall total from January to July as an indicator of the break in the seasonal summer drought, which normally breaks in March or April, and of sufficient winter rains.

The sampling was done in August 2005. I studied species health at nine locations in the Agter-Cedarberg, a mountain valley North of the Cedarberg range, about 30 kilometres east of Clanwilliam, in the Western Cape, 400 kilometres north of Cape Town. Species health data was obtained by walking along 100m transects, noting the health status of all individuals of all species present within 1m on both sides of the transect. All woody shrubs and trees, as

well as common restios and mesembs, were sampled. The transects were located as indicated on **Map 2** (map of the Agter-Cedarberg).

I sampled along an altitudinal gradient, from 250m to 900m (**Appendix 1**). At each site I located nearby patches with rocky or sandy substrate, and sampled a transect on each substrate. Site 2 was a riparian site and was not suitable for transect sampling, so instead all accessible groups of plants within a small area were sampled. Data collected here is useful as surrogate control for want of a real control.

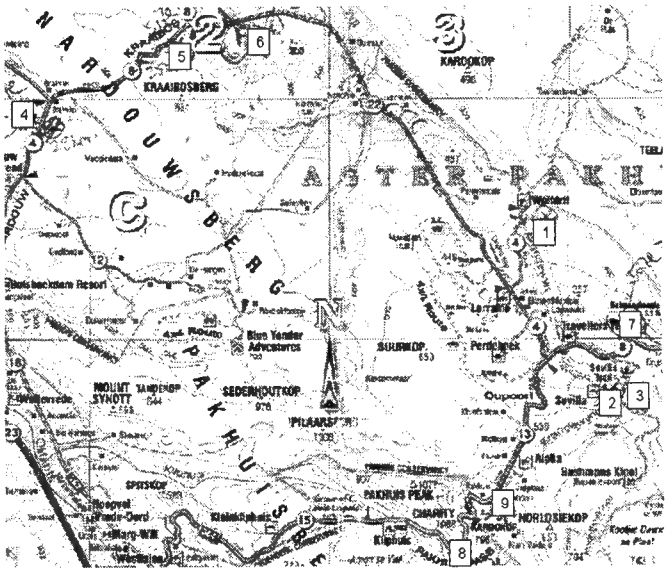

Figure 1. Map of the Agter-Cedarberg (also known as Agter Pakhuis), with numbers showing the study sites. Scale 5cm:1km. (reproduced from Slingsby 2003 Map of the Cederberg).

Health status was based on extent of canopy death: less than 50% canopy death was assigned to category 2 – 'healthy', more than 50% to canopy death to 1 – 'sick', and total canopy death to 0 – 'dead'. Grasses, geophytes and annuals were not sampled. Species health was calculated per transect as the frequency of observations in each category (later referred to as f(0), f(1) and f(2)).

For stem anatomy, I collected twig cuttings of the most common woody shrubs at various sites, about 20-30cm long and 4-8mm wide. These were kept in a fridge at 10°C for 3 weeks until use. I pressed specimens of each species sampled, for identification and referencing.

I measured stem vessel diameter and density by boiling the stems for 2-4 hours to soften them after which 30micron sections were made using a Reichert Jung

base sledge microtome. I made about 10 sections per species and mounted them in glyerol on laboratory slides. I took 15 photographs per species, choosing the clearest sections to photograph. Only the largest vessels, near the outer edge of the stem, were measured, as the largest vessels conduct water most efficiently (Zimmerman 1983) and are thus the most important to measure. I measured tangential vessel diameters of 30-50 vessels per species using the measurement software SIGMASCAN. As the photos were all taken at the same total magnification (400x), on the camera's maximum zoom-out, the dimensions of the images were relative. I counted the number of vessels per photograph (generally the whole photograph was of stem tissue) and used this as a surrogate for stem conductivity. I constructed an index for relative conductivity by multiplying tangential vessel diameter (TVD) by vessels per photo (VPP): this is the conductivity index (CI).

Statistical analyses were done in STATISTICA 7 and Microsoft EXCEL XP. To analyse the effect of altitude and substrate on species health I used the general linear model (GLM) function in STATISTICA 7. Single factor analysis of variance (ANOVA) was used to detect difference between species in tangential vessel diameter. I used a correlation matrix (r-values) to detect correlations between species health and tangential vessel diameter, vessels per photo and conductivity index.

This study was initiated in response to the altered state of the vegetation in the Agter-Cedarberg. As such, there was no prior opportunity to institute an experimental design with controls. An ideal control would entail sampling of the same sites under prior 'normal' rainfall conditions. Such pre-emptive sampling is important when current bioclimatic models predict changes in specific areas.

Results

Rainfall analysis

By relating the rainfall for 2003 and 2004 to the long-term record, I found that these years together and separately constituted critical drought. Total annual rainfall in 2003 was the sixth lowest on record at Clanwilliam (1870-2005) (55% of the mean, **Table 1**, **Figure 4**), and the fifth lowest at Mertenhof (1898-2005) (47% of the mean, **Table 2**, **Figure 5**). At Mertenhof 2004 was also severe, being the seventh worst year on record (52% of the mean, **Table 2**, **Figure 5**). The summer drought breaks on average in March or April and rainfall peaks in June (**Figure 1**), so the January to July average (**Figure 6** for Clanwilliam, **Figure 7** for Mertenhof) should reflect any failures of the summer drought to break. In both places 2003 had the lowest January to July rainfall on record (11.7% for Clanwilliam and 20% for Mertenhof, **Figure 6** and **Figure 7**).

Species Health analysis

In assessing species health, I found that most of the vegetation was healthy (67% across all species, and 65% for the abundant species only (those found at more than three sites, and of which more than 30 observations were made; **Figure 8**). Mortality was higher on sandy soils (All species: general linear model 1-sided t-test: t=-2.87, **p=0.004**, **Table 5**; **Figure 9**; Abundant species: general linear model 1-sided t-test: t=-2.68, **p=0.01**, **Table 7**; **Figure 12**).

Altitude was a highly significant predictor of all three health categories, for all the data (**Table 5**: f(0), t=7.65, **p<0.000**; f(1), t=9.9, **p<0.000**; f(2), t=26.81, **p<0.000**). Frequency of healthy individuals increased with altitude (R^2=0.0236; R=0.1536, p=0.0105, **Figure 10**) and frequency of dead individuals decreased with altitude, (R^2 =0.0400, R= -0.1999, **p = 0.0008**, **Figure 11**) for all data.

For the abundant species separately, only soil type was a significant predictor of species health (F=3.80, **p=0.0249**, **Table 6**). Only the frequency of dead individuals was predicted (general linear model t-test: t=-2.68, **p=0.01**, **Table 7**).

Mortality was twice as high on sand as opposed to rocky soils (range: 0.06 to 0.16 for rocky soils, 0.16 to 0.34 on sandy soils, **Figure 12**). Altitude was a less significant predictor of frequency of dead individuals (general linear model t-test: t=-1.80, p=0.07). Mortality was lower at higher altitudes, although the relationship was weak and not significant at the five percent significance level (R^2 =0.0236, p=0.0848). The worst affected were *Aspalathus*, with 35% mortality, *Passerina*, with 32% mortality, *Nylandtia spinosa* with 24% mortality, and *Phylica sp.* with 10% mortality (**Table 11**).

Overall, although the relationships are weak, both altitude and soil type are significant predictors of species health.

Road Transect

The roadside survey covered 30km, covering a total area of about 1.5km^2. The veld condition was generally poor, ranging from very poor to mostly healthy. More than 10% of the veld was healthy, and more than 5% was dead (**Figure 14**).

Riparian Site

The riparian trees and shrubs at site 2 ranged from very healthy (*Brachylena neriifolia,* 7% canopy death, *Euclia linearis*, 6%) to dead (*Euclea tomentosa* and *Rhus lucida*) (**Figure 15**). Seven out of the ten species sampled had more than 50%, and three less than 20% canopy death.

Vessel analysis

Vessel diameters (in microns, mean±variance) ranged from 42±60 in *Aspalathus sp.* to 21±4 in *Nylandtia spinosa* (**Table 9**). The analysis of variance revealed a highly significant difference between species (F=86, **p<0.000**, **Table 10**). Vessels per photo ranged from 11 in *Phylica sp.* to 49 in *Elytropappus rhinocerotus* (**Table 11**). Conductivity index (vessel diameter multiplied by

vessels per photo) ranged from 370 in *Phylica* to 1515 in *Elytropappus rhinocerotus* (**Table 11**).

There were no correlations between species health and vessel diameter, vessels per photo or conductivity index (**Table 12**). The only interesting correlations in the data were between the health frequencies (between healthy and sick, r=-0.84, p=0.005; dead and healthy, r=-0.90, p=0.001), and a weak negative correlation at the 10% significance level between vessel diameter and vessels per photo (r=-0.58, p=0.098, **Table 12**).

Discussion

Drought in the Southern Hemisphere is predicted to increase in severity and duration in the next 50 years, due to climate change (Midgley *et al* 2001). Droughts such as that of 2003/2004, which was a 1:100 year occurrence, could become commonplace. How will the fynbos biome respond if this occurs?

The results of this study show that, on the whole, fynbos in the Agter-Cedarberg coped well with the drought, suffering relatively little mortality. There was high mortality in localised patches, and species showed varying levels of mortality. Higher altitudes offered some protection, as did rocky soil as opposed to the lowland deep sandy soils. This is an important result for conservation planning and reserve selection, as not all current reserves may have sufficient altitudinal gradients and rocky habitats. Also, areas which were previously not regarded as important for conservation may be so in the light of climate change.

As most fynbos occurs on lowland sandy plains, these result suggest that most fynbos will experience great stress during future droughts. The relationship between altitude and mortality was very weak, though – mortality was not much lower at higher altitudes. So, there may not be that much benefit of being at higher altitude. Bioclimatic models predict that fynbos will be limited to mountainous regions in the Southern Cape, with a much smaller range than at

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present (Midgley *et al.* 2003). If the relationship between species health and altitude is as weak in reality as this study suggests, the models may be under-estimating the threat.

The riparian site was used to gain an impression of the vegetation of the area under more favourable moisture conditions. However, the results show that the trees sampled were in even worse condition than the vegetation at the other sites. Riparian trees are shallow rooted, which is possible since they have access to a high water table. As a result, they will suffer all the more when the water table drops, as happened during the 2003/2004 drought. Non-riparian plants typically have deep root systems, or shallow roots that capture ephemeral rains. The riparian site, rather than providing a control for the study, is a warning signal about the risk to riparian ecosystems from drought. These ecosystems occupy a small geographical area relative to the fynbos biome and are worth making a focus of conservation efforts.

The road transect method for sampling drought impacts on the vegetation produced results which are less positive than the species health analysis. Sixty percent of the area observed, which represented most of the valley, was in poor condition or worse. This discrepancy is related to the composition of the vegetation: most areas are dominated by a few large shrub genera or species (*Phylica sp.*, *Nylandtia spinosa*, *Passerina sp.* and *Aspalathus sp.*) which are highly visible from the road, and which generally showed higher drought mortality than the smaller less visible species. This method of impact assessment is easy and can be done by non-trained staff, so it is attractive as a rapid drought measurement system. However, the results here show that it must be interpreted with caution, as it can misrepresent the condition of the vegetation.

The worst-affected genus, *Aspalathus*, may provide a useful 'early warning system' for drought monitoring, as it appears highly sensitive to water stress. The order in which genera and species start to show signs of drought stress or

mortality could be used to construct a model for measuring drought severity and impacts in fynbos.

How should future droughts and climate change be tackled, in the light of this study? The fact that very high mortality (more than 20%) was only found in one third of the common species (3 out of 9) is encouraging. However, the impacts may be worse for less common and rare plants. The effort required to sample sufficient numbers of these for a similar analysis is beyond the scope of small studies. However, it is critical if we are to understand the future of fynbos, as much of the diversity of fynbos rare and endemic.

What is the future for fynbos in the face of climate change? This study suggests that community composition in current fynbos regions may change, with some common large woody shrubs dying out. Possibly a few tolerant shrubs, such as *Wiborgia sericea* and *Dodonea purpurea*, may become dominant in the overstorey.

The physiological aspects investigated here, namely vessel diameter, vessel density and conductivity index, were unrelated to species health or mortality. This suggests that drought tolerance in these species is determined by other factors, for example rooting depth, vessel wall strength or leaf morphology. However, the species with the largest vessels, *Aspalathus*, also had the highest mortality. In contrast, the second largest vessels were found in a species with very low mortality, *Rhus glauca*.

Drought impacts on vegetation in South Africa need to be studied, if we are to conserve biodiversity efficiently. This study shows that impacts one year after a severe drought are not as severe as might be expected, giving some hope. Effects of drought are localised, and differ widely between species. Physiological studies of drought tolerance in fynbos species are critical, as they can highlight species which will be unable to cope with future conditions, as well as being

unable to disperse to suitable habitat. Efforts must be made now to identify such species, so that their genetic material can be fully sampled for conservation in reserves and botanical gardens.

Climate change and drought are realities in South Africa. The future of our biodiversity is at stake. Areas that may be at risk should be sampled now, before worse droughts, and their biodiversity mapped. This will provide invaluable 'before and after' comparative data, when severe droughts occur. This type of study will help enormously in conservation efforts.

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Tables and Figures

Table 1. The lowest five years of total annual rainfall at Clanwilliam, from 1879 to 2004. The lowest year was 1969, and the 5th lowest was 2003.

Year	Rainfall (mm)	% of mean
1969	85	**41%**
1928	90	43%
1896	109	52%
1927	111	53%
2003	115	**55%**

Table 2. The lowest seven years of total annual rainfall at Mertenhof Farm in the Biedow Valley, from 1898 to 2004. The lowest year was 1960. The years 2003 and 2004 were the 6th and 8th lowest years respectively.

Year	Rainfall (mm)	% of mean
1960	69	**31%**
1928	73	33%
1927	82.6	37%
1926	100.2	45%
1924	103.7	46%
2003	106.4	**47%**
1958	115.5	52%
2004	115.5	**52%**

Table 3. Species health varied with altitude and soil type for all data, when analysed by a general linear model. Df=degrees of freedom.

	Test	Value	F	Effect df	Error df	p
Altitude	Wilks	0.12	665.29	3.00	273.00	**0.0000**
Soil Type	Wilks	0.97	2.78	3.00	273.00	**0.0414**

Table 4. Variance in species health as described by the general linear model, for all data. All the variance was significant (species health varied with the altitude). f(2)= healthy, f(1)=sick, f(0)=dead.

	Adj'd R^2	MS Model	SS Residual	df Residual	MS Residual	F	p
F(0)	0.18	2.11	18.15	275	0.07	32	**0.000**
F(1)	0.26	4.31	23.87	275	0.09	49	**0.000**
F(2)	0.72	57.42	43.51	275	0.16	362	**0.000**

Table 5. Frequency of dead and healthy individuals was predicted by altitude and soil type, and frequency of sick individuals was predicted by altitude, for all data. f(2)= healthy, f(1)=sick, f(0)=dead.

	Health categ.	Param.	SE	t	p	Beta (ß)	St.Err.ß
Altitude	f(0)	0.00	0.00	7.65	**0.000**	0.42	0.05
Soil Type (rocky)	f(0)	-0.04	0.02	-2.87	**0.004**	-0.16	0.05
Altitude	f(1)	0.00	0.00	9.90	**0.000**	0.51	0.05
Altitude	f(2)	0.00	0.00	26.81	**0.000**	0.85	0.03
Soil Type	f(2)	0.02	0.02	0.72	0.471	0.02	0.03

Table 6. For the abundant species, only soil type was a predictor of species health.

	Test	Value	F	Effect	Error	p
Altitude	Wilks	0.97	1.68	2	123	0.1901
Soil Type	Wilks	0.94	3.80	2	123	**0.0249**

Table 7. The frequency of dead individuals was predicted by soil type, and predicted by altitude but not at the 5% level, for the abundant species.

	Param.	SE	t	p	Beta (ß)	St.Err.ß
Altitude	-0.0002	0.00	-1.80	**0.07**	-0.16	0.09
Soil Type	-0.0631	0.02	-2.68	**0.01**	-0.23	0.09

Table 8. Abundant species only: species in >3 sites, with >30 observations)

	Observations	**# sites**
Wildenowia incurvata	270	6
Ruschia sp.	241	5
Aspalathus sp	95	5
Nylandtia spinosa	402	8
Disperago sp.	234	5
Anthospermum sp.	34	6
Phylica spp.	164	7
Elytropappus rhinocerotus	97	4
Rhus glauca	88	8
Wiborgia sericea	146	3

Table 9. Average vessel diameter and variance for the nine fynbos species sampled at the Agter-Cedarberg, after the 2003/2004 drought. Units are microns.

Groups	Count	Sum	Average	Variance
Aspalathus spp.	33	1407.86	42	60
Rhus glauca	33	1328.208	40	18
Euryops spp.	33	1290.079	39	44
Phylica spp.	33	1110.128	33	36
Elytropappus rhinocerotus	33	1020.458	30	4
Passerina spp.	33	749.3985	22	2
Nylandtia spinosa	33	725.9192	21	4
Dodonea purpurea	33	707.053	21	9
Wiborgia sericea	33	1015.967	30	49

Table 10. The analysis of variance of tangential vessel diameter (microns), of woody fynbos species from the Agter-Cedarberg, after the 2003/2004 drought.

Source of Variation	*SS*	*df*	*MS*	*F*	*P-value*	*F crit*
Between Groups	17598.45	8	2199.80	86.08	**0.0000**	1.97
Within Groups	7359.70	288	25.55			
Total	24958.15	296				

Table 11. Health, vessel diameter and conductivity index means for abundant species of fynbos plants collected at the Agter-Cedarberg, after the 2003/2004 drought. TVD=tangential vessel diameter, VPP=vessels per photo, CI=conductivity index. f(2)= healthy, f(1)=sick, f(0)=dead.

Species	f(2)	F(1)	F(0)	TVD	VPP	CI	n	Sites
Rhus glauca	0.92	0.06	0.02	40.25	15	604	88	8
Dodonea purpurea	0.93	0.04	0.03	21.43	24	514	21	4
Elytropappus rhinocerotus	0.84	0.11	0.06	30.92	49	1515	97	4
Phylica sp.	0.79	0.11	0.10	33.64	11	370	195	7
Euryops sp.	0.63	0.28	0.08	39.09	15	586	120	3
Nylandtia spinosa	0.53	0.23	0.24	22.00	33	726	402	8
Passerina sp.	0.60	0.08	0.32	22.71	34	772	267	4
Aspalathus sp.	0.38	0.27	0.35	42.66	11	469	178	6
Wiborgia sericea	0.96	0.02	0.02	30.79	15	462	146	3

Table 12. There were no correlations between vessel characteristics and species health for abundant species of fynbos plants collected at the Agter-Cedarberg, after the 2003/2004 drought. TVD=tangential vessel diameter, VPP=vessels per photo, CI=conductivity index. Correlation coefficients are in italics. f(2)= healthy, f(1)=sick, f(0)=dead.

	F(1)	F(0)	TVD	VPP	CI
F(2)	*-0.8392*	*-0.9029*	*-0.1553*	*0.0256*	*0.0671*
	p=0.005	**p=0.001**	p=0.690	p=0.948	p=0.864
F(1)		*00.5247*	*0.3866*	*-0.1292*	*-0.0345*
		p=0.147	p=0.304	p=0.740	p=0.930
p(D)			*-0.0628*	*0.0831*	*-0.0520*
			p=0.872	p=0.832	p=0.894
TVD				*-0.5851*	*-0.1925*
				p=0.098	p=0.620
VPP					*0.9009*
					p=0.001

Rainfall Figures

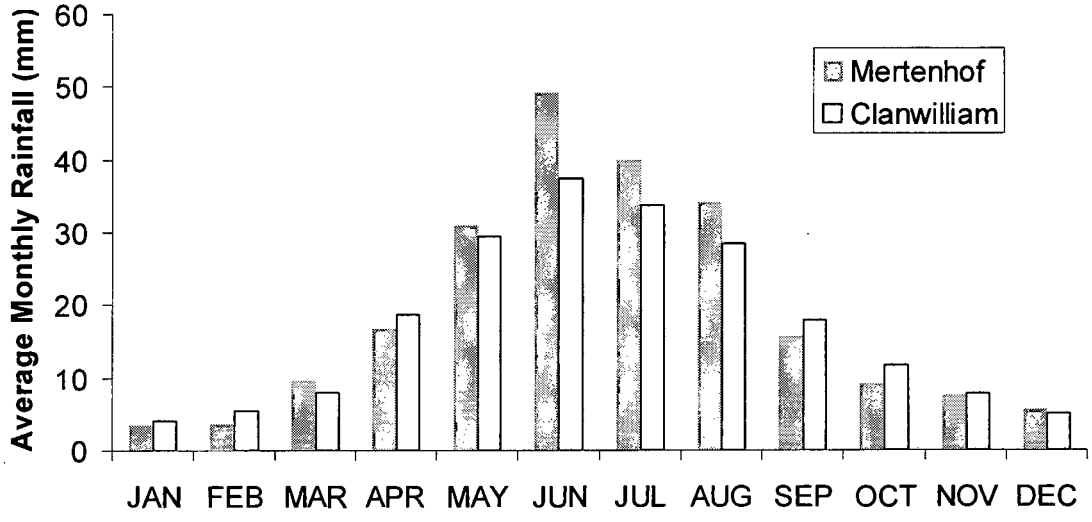

Figure 3. The average monthly rainfall at Mertenhof (1898-2004) and Clanwilliam (1870-2004), in the Western Cape, South Africa.

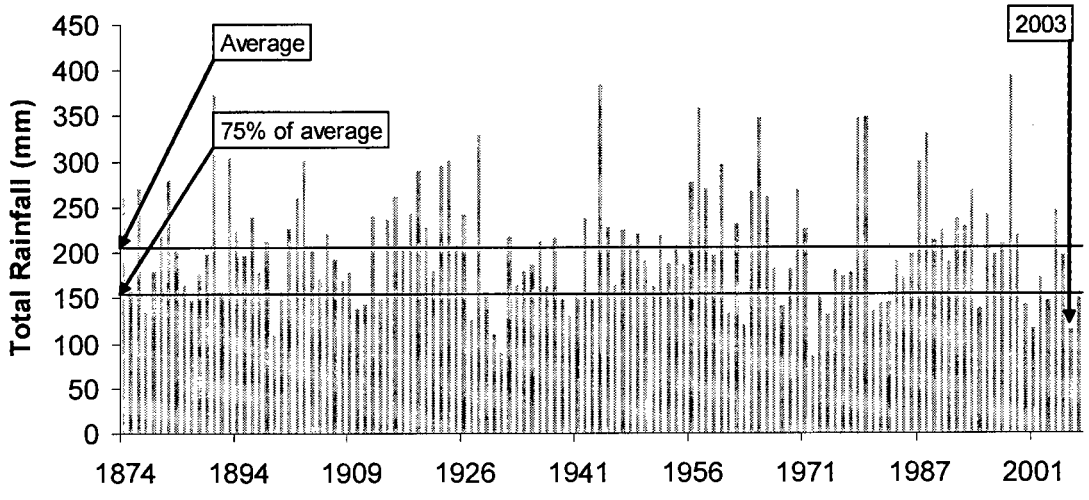

Figure 4. Total annual rainfall at Clanwilliam has been below 75% of the mean on 26 occasions from 1870 to 2004. The year 2003 was the fifth lowest, and 1999 was the 6th lowest (see **Table 1**).

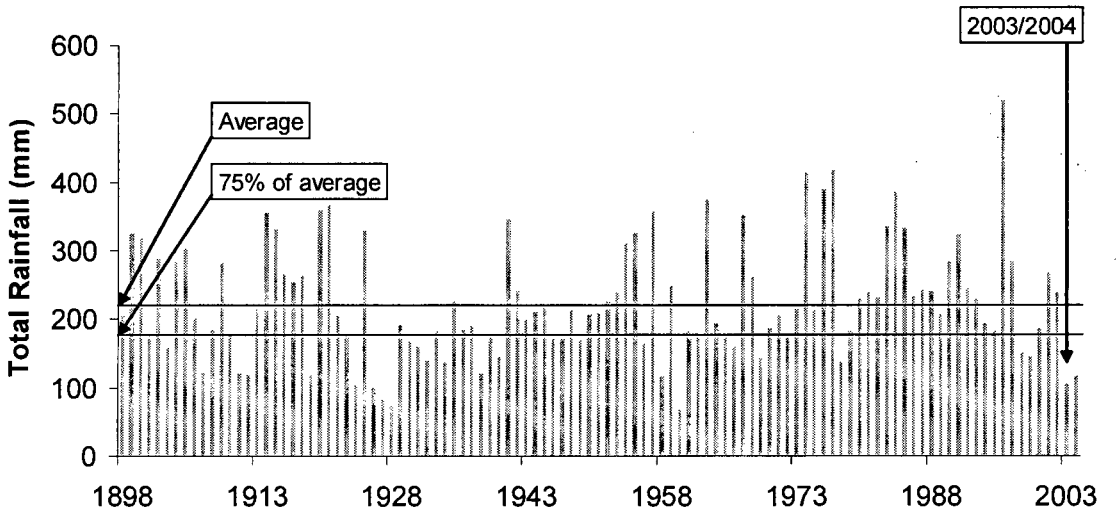

Figure 5. Total annual rainfall at Mertenhof has been below 75% of the mean on 25 occasions from 1889 to 2004. The year 2003 was the 6th lowest, and 2004 was the 8th lowest (see **Table 2**).

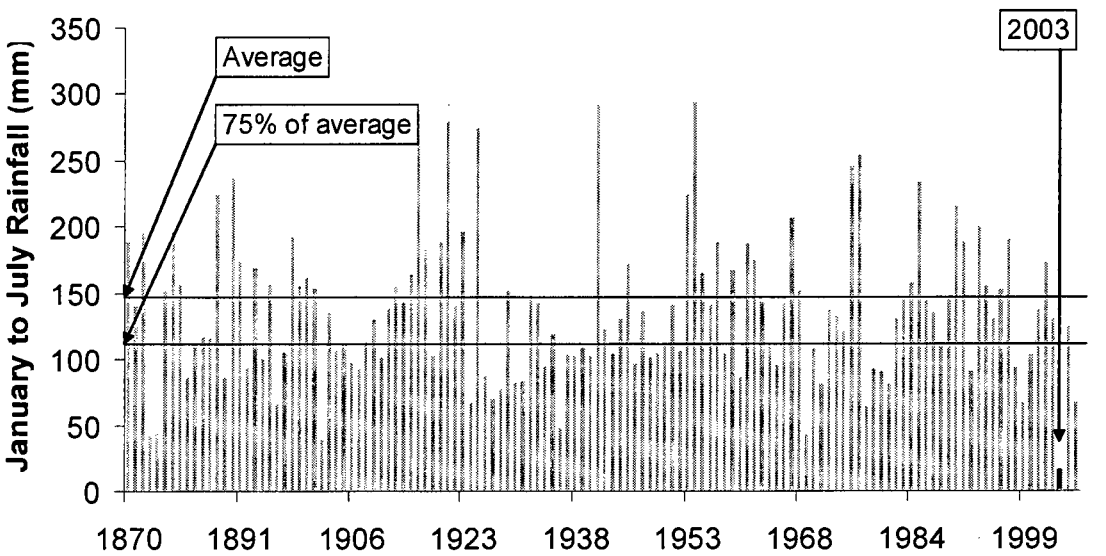

Figure 6. The summer drought in the winter rainfall region of Clanwilliam (1870-2005) breaks between March and April, and rainfall peaks in June. Hence the January to July total rainfall figures should reflect failures of the summer drought to break. The lowest year was 2003, which received 11.7% of the mean rainfall.

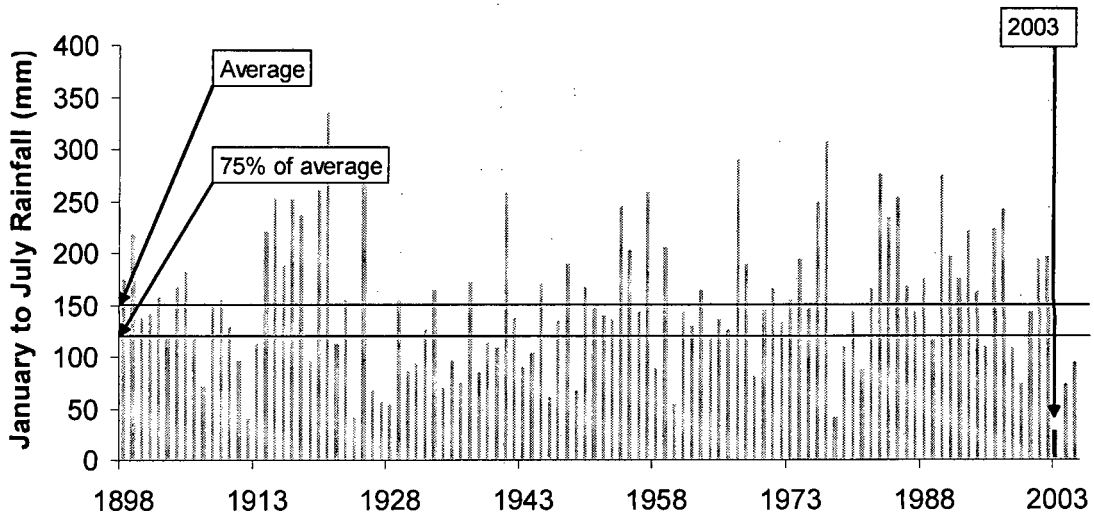

Figure 7. The summer drought in the winter rainfall region of Mertenhof breaks between March and April, and rainfall peaks in June. Hence the January to July total rainfall figures reflect failure of the summer drought to break. The record is from 1898 to 2005. In 2003, 20% of the mean rainfall occurred.

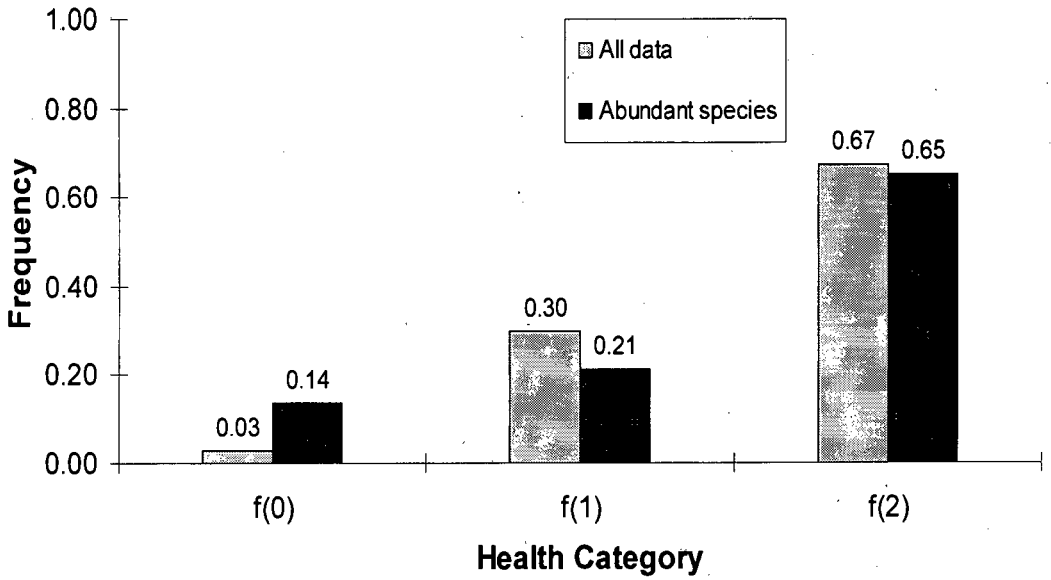

Figure 8. The frequency of healthy individuals was far greater than that of sick or dead individuals, for both the 'abundant' species only (those found at more than three sites, and of which more than 30 observations were made) and for the entire data set. f(2)= healthy, f(1)=sick, f(0)=dead.

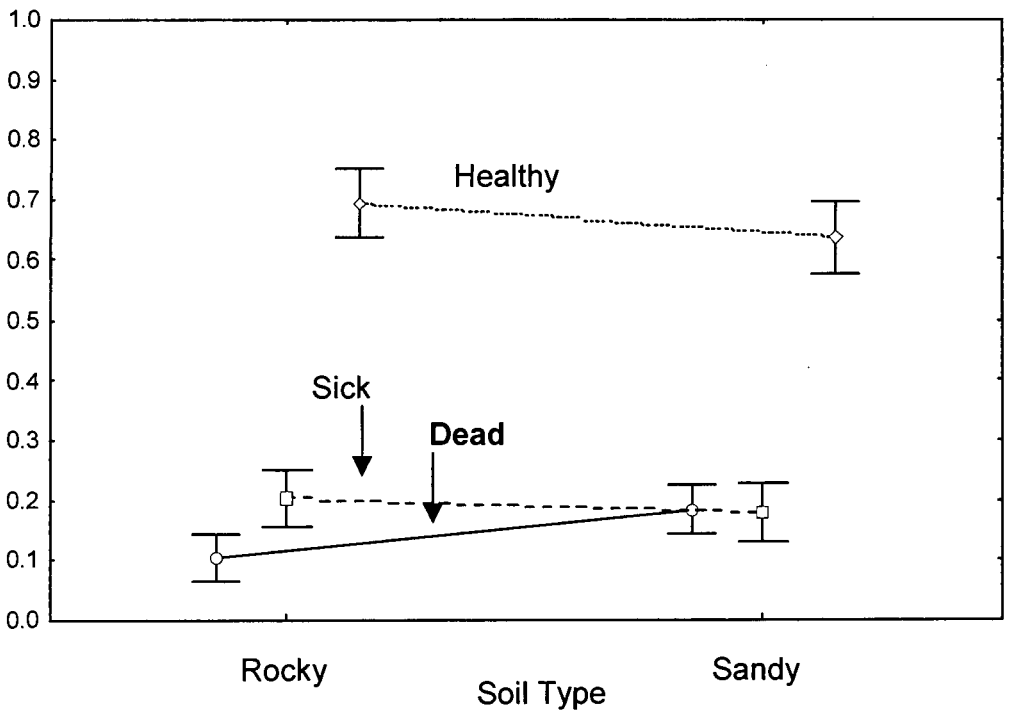

Figure 9. The mean frequency of dead individuals of fynbos plants was lower on rocky than on sandy soils following the 2003/2004 drought in the Agter-Cedarberg. Bars are 95% confidence limits around the mean. **Dead individuals**: Kruskall Wallis ANOVA by ranks: H(1,127) = 5.81, **p = 0.0159**; F(1,125) = 6.99, **p = 0.0092**.

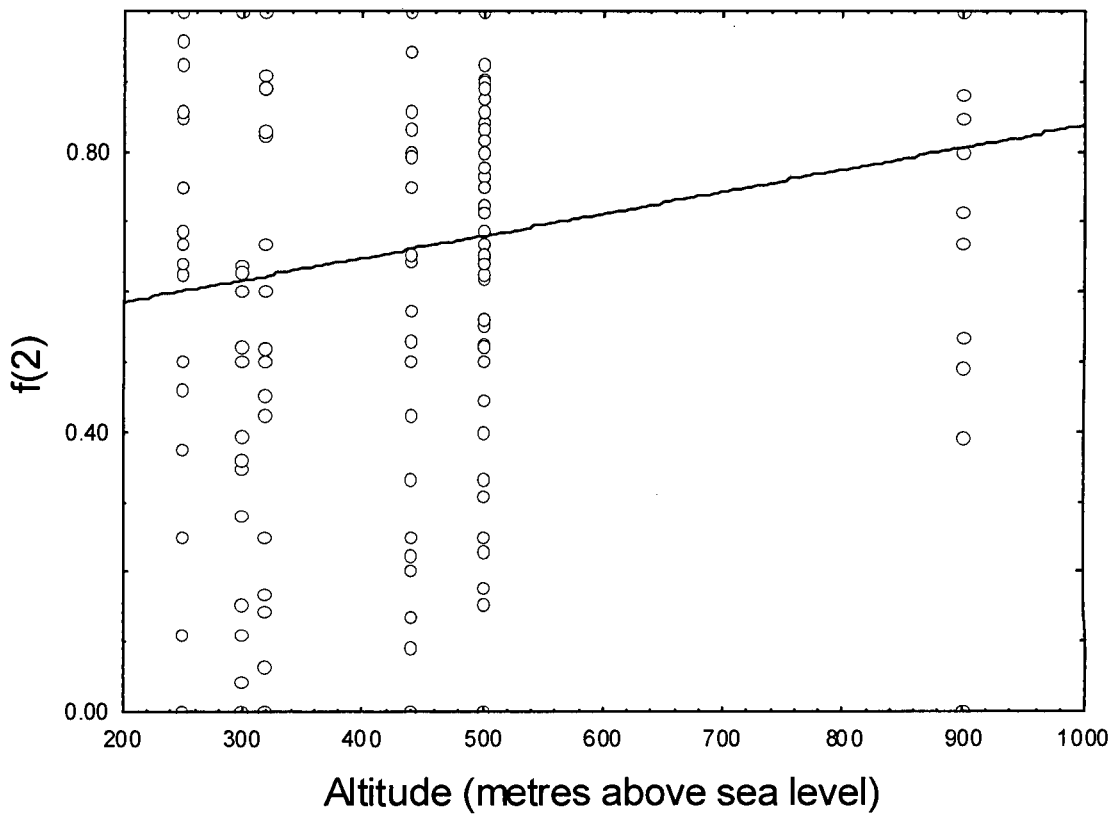

Figure 10. The frequency of healthy individuals of fynbos plants was higher at higher altitudes, following the 2003/2004 drought in the Agter-Cedarberg. R^2 = 0.0236; R= 0.1536, p = 0.0105. f(2)= healthy.

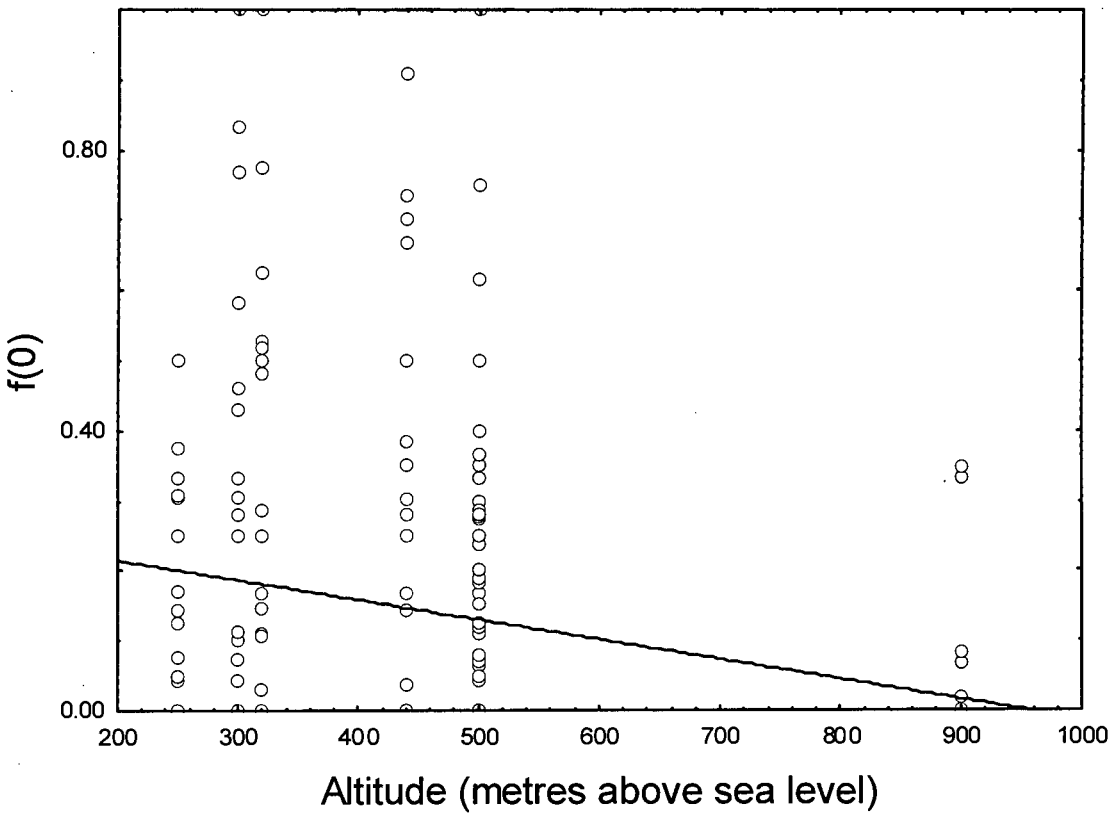

Figure 11. The frequency of dead individuals of fynbos plants was lower at higher altitudes, following the 2003/2004 drought in the Agter-Cedarberg. R^2 =0.0400, R= -0.1999, p = 0.0008. f(0)=dead.

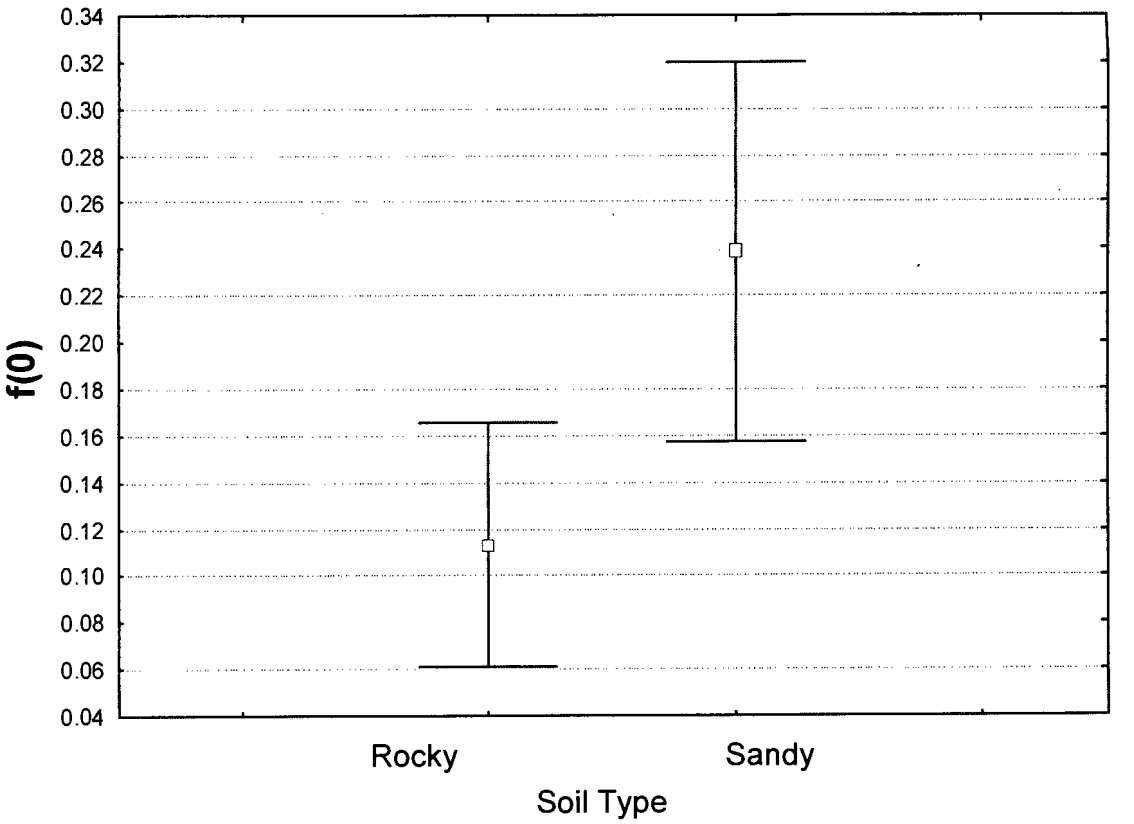

Figure 12. When the 'abundant' fynbos plant species (see **Figure 8**) were analysed separately, the frequency of dead individuals was still found to be lower on rocky soils than on sandy soils, while the difference was not significant for healthy individuals. Kruskall Wallis: H(1,127) = 5.8138, p = 0.0159. f(0)=dead.

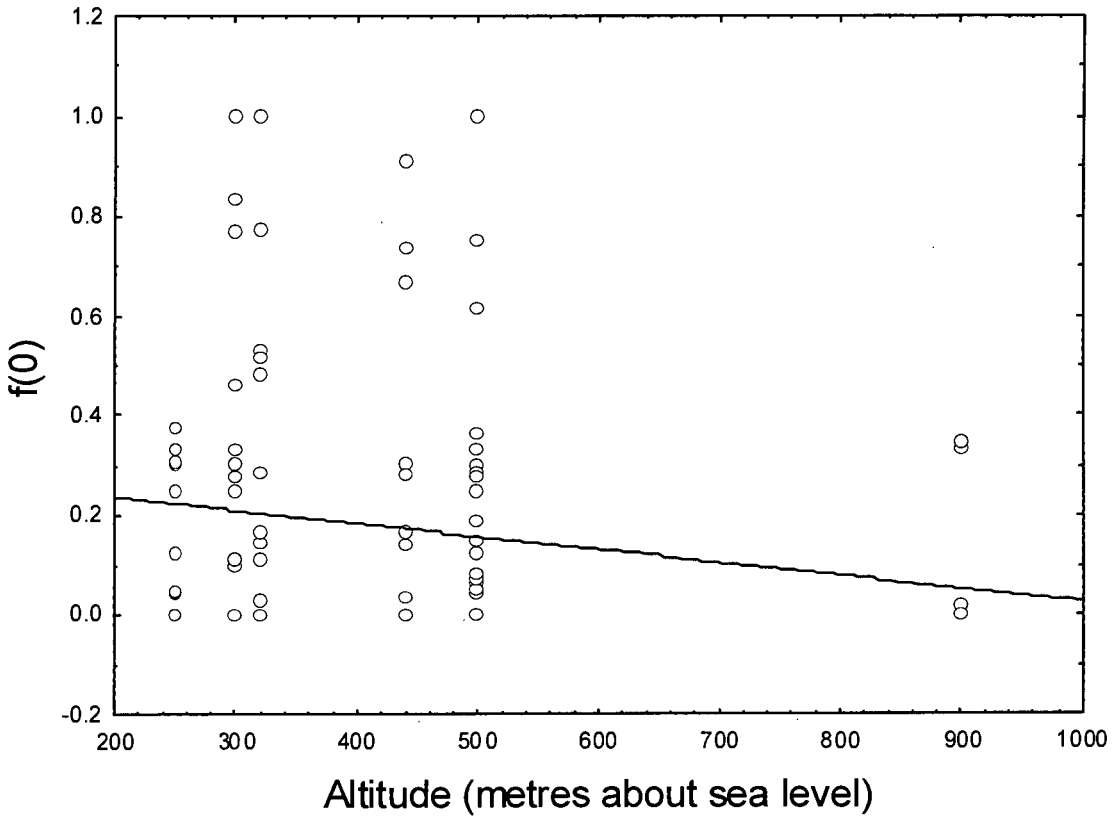

Figure 13. The frequency of dead individuals of the 'abundant' species (see **Figure 8**) of fynbos plants was lower at higher altitudes, following the 2003/2004 drought in the Agter-Cedarberg (although the relationship is not significant at the 5% level: : R^2 =0.0236.; R= -0.1536, p = 0.0848. f(0)=dead.

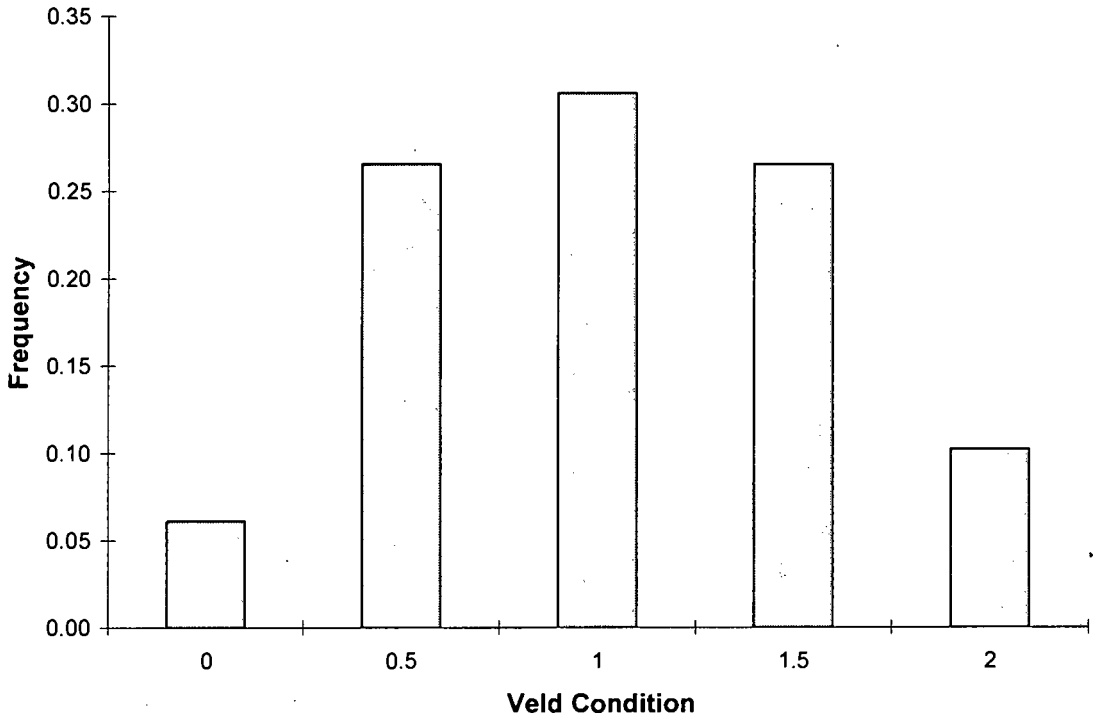

Figure 14. Condition of the veld observed from car during road-side transects. Veld condition: 0=dead, 0.5=very poor, 1=poor, 1.5=mostly healthy, 2=healthy. Total distance covered was 30km, and area surveyed was from 50m away from road for another 50m. Total area surveyed was approximately 1.5km^2.

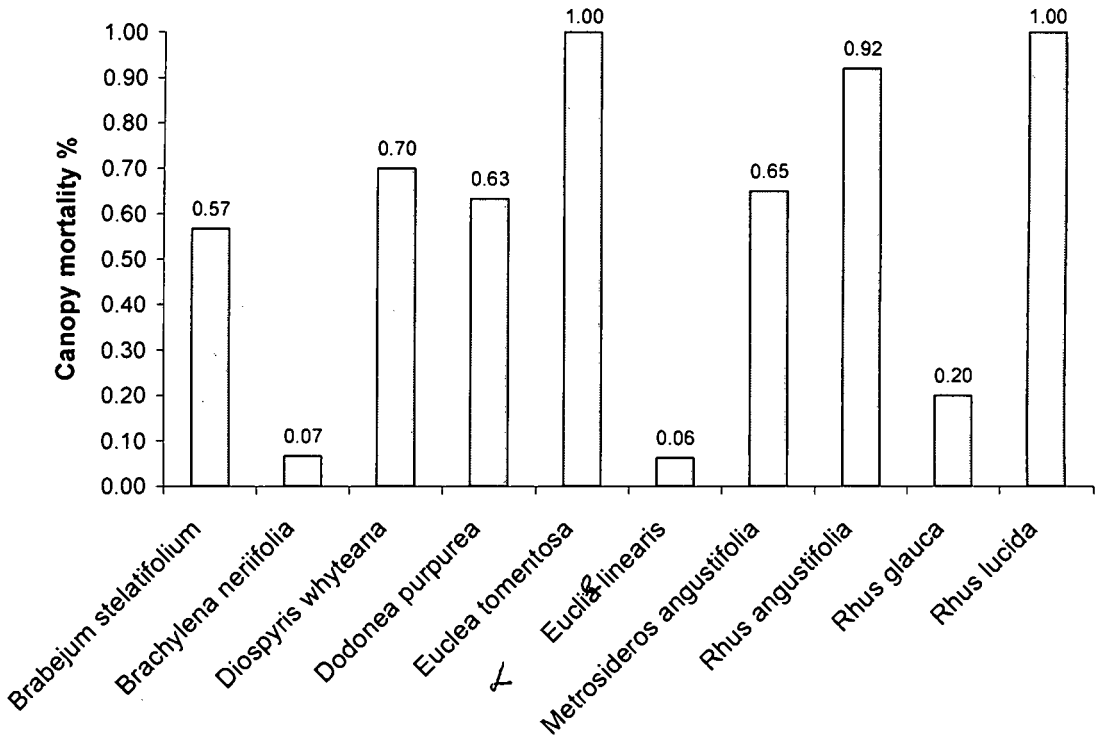

Figure 15. Canopy mortality at the riparian site (site 2) was highly variable, ranging from complete to low mortality. Between 5 and 10 trees were sampled per species.

Appendix 1. Altitudes at each site sampled.

site	altitude	site	altitude
6	250	5	500
1	300	7	500
2	300	9	500
3	320	8	900
4	440		